DRUG DISCRIMINATION UNDER A CONCURRENT FIXED-INTERVAL FIXED-INTERVAL SCHEDULE

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Pigeons were trained to discriminate 5.0 mg/kg pentobarbital from saline under a concurrent fixedinterval (FI) FI schedule of food presentation on which, after pentobarbital administration, responses on one key were reinforced with food under an FI 60-s component and responses on the other key were reinforced under an FI 240-s component. After saline administration, the schedule contingencies on the two keys were reversed. After both pentobarbital and saline, pigeons responded more frequently on the key on which responses had been programmed to produce the reinforcer under the FI 60 component of the concurrent schedule. The schedule was changed to concurrent FI 150 FI 150 s for drug-substitution tests. In each bird, increasing doses of pentobarbital, ethanol, and chlordiazepoxide produced increases in the proportion of responses on the key on which responses had been reinforced under the FI 60 component after pentobarbital administration during training sessions. The proportion of responses on that key was slightly lower for ethanol than for chlordiazepoxide and pentobarbital. At a dose of pentobarbital higher than the training dose, responding decreased on the key that had been reinforced under the FI 60 component during training sessions. Phencyclidine produced less responding on the key programmed under the FI 60-s component than did pentobarbital. Methamphetamine produced responding primarily on the key on which responses had been reinforced under the FI 60-s component after saline administration.

Key words: drug discrimination, concurrent fixed-interval schedules, matching law, drugs, key peck, pigeons

One of the most important determinants of drug effects in behavioral pharmacology is the schedule of reinforcement that maintains responding (Kelleher & Morse, 1964), but the effects of the reinforcement schedule have received little attention in drug-discrimination experiments. Recent experiments from our laboratory have suggested that the schedule of reinforcement is also a powerful determinant of the effects of drugs in drug-discrimination experiments (Massey, McMillan, & Wessinger, 1992; Snodgrass & McMillan, 1991, 1996).

The usual procedure in drug-discrimination experiments is to reinforce responses under a fixed-ratio (FR) schedule of reinforcement on only one response key if a drug has been administered before the session (drug key) and to reinforce responses under the same schedule on a different key if the drug vehicle has been administered before the session (saline key). Responses on the inappropriate key never produce the reinforcer and

may reset the contingency on the "injectionappropriate" key. Investigators usually have reinforced responding under identical FR schedule values after administration of both drug and vehicle (Colpaert, 1987), although fixed-interval (FI) schedules (Krimmer, McGuire, & Barry, 1984; Massey et al., 1992), variable-interval (VI) schedules (Gouvier, Akins, & Trapold, 1984), tandem schedules (Witkin, Carter, & Dykstra, 1980), multiple schedules (McMillan & Hardwick, 1996; Snodgrass & McMillan, 1991), second-order color-tracking schedules (McMillan, Cole-Fullenwider, Hardwick, & Wenger, 1982), and concurrent schedules (Snodgrass & McMillan, 1996) have also been used. Usually these schedules have been symmetrical, in that responding on the drug key after drug administration and responding on the saline key afvehicle administration have been reinforced using the same schedule values. However, it has been shown that responding can be biased toward responding on either the drug or the saline key by manipulation of the schedule of reinforcement (Koek & Slangen, 1982; McMillan & Wenger, 1984).

If the schedule of reinforcement is an important determinant of stimulus control in drug-discrimination experiments, it is likely

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that the shape of the generalization curve when other drugs are substituted for the training drug will also depend on the schedule of reinforcement during discrimination training sessions. There has been considerable discussion about the relationship between dose and response in drug-substitution experiments (Colpaert, 1986). Most investigators have assumed that there is a quantitative relationship between dose and response, so that the dependent variable (e.g., percentage of responses on the drug key) is measured on a continuous scale. When responding on the drug key is measured on a continuous scale, the proportion of responses on the drug key after a dose of drug is usually considered to be a measure of the degree to which that dose is similar to the training dose. However, there are also those who maintain that the relationship between dose and response is a quantal unit that does not vary (Mathis & Emmett-Oglesby, 1990). According to this viewpoint, the subject detects either the presence or absence of the training dose when a drug is given; thus, responding is measured on a nominal scale. Another possibility is that whether responding in drugdiscrimination experiments is nominal or continuous depends on the schedule of reinforcement. Holloway and Gauvin (1989) have suggested that schedules that bias subjects to maximize reinforcement in choice situations by confining responses to one alternative (e.g., simple FR schedules) generate nominal responding, whereas schedules that maximize reinforcement when animals distribute their responses according to the matching law (Herrnstein, 1970, 1974) favor a graded distribution of responding across both response alternatives (e.g., VI schedules).

These suggestions are consistent with the data from our comparison between the effects of FI and FR schedules of reinforcement on the form of the generalization gradient (Massey et al., 1992; Snodgrass & McMillan, 1991). We found that graded responding occurred when responding was maintained under FI schedules and nominal responding occurred when responding was maintained under FR schedules using both morphine and pentobarbital as training drugs. However, typically a drug discrimination is established by reinforcing "correct" responses and by ex-

tinguishing "incorrect" responses under the appropriate stimulus conditions. Thus, as Colpaert (1986) has noted, the discrimination is established under "all-or-none" reinforcement contingencies, which might be expected to favor nominal responding.

Although it is generally true in practice that responding on the incorrect key is not reinforced, this is not a necessary condition for establishing drug discrimination, because we have shown that drug discrimination can be established under conditions of relative reinforcement (Snodgrass & McMillan, 1996). This was done by reinforcing responding under concurrent VI VI schedules of reinforcement, on which the values of the component VI schedules provided different frequencies of reinforcer delivery. After administration of the training drug, responding on both keys was reinforced. However, there was a difference in the schedule of reinforcer delivery for responding on the two keys, with the schedule associated with the drug-biased key (key that was programmed at the higher reinforcement density after drug administration) providing a 4:1 ratio of reinforcers compared to the schedule associated with the vehicle-biased key (key that was programmed at a higher reinforcement density after vehicle administration). After saline administration, the reinforcement schedules programmed on the two keys were reversed. Thus, under the concurrent schedule, reinforcement contingencies were relative in contrast to the all-or-none contingencies that are usually employed in drug-discrimination experiments.

We were successful in establishing drug discrimination under concurrent VI VI schedules (Snodgrass & McMillan, 1996). In these experiments, pigeons responded about 70% of the time on the key on which responses could produce the reinforcer more frequently, which is close to the proportion of responses that the matching law predicts would occur on that key. The procedure has several potential advantages. First, the use of the concurrent schedule provided an opportunity to integrate drug-discrimination data with the matching law (Herrnstein, 1970). According to the matching law, under concurrent interval schedules of reinforcement, response percentages approximately match reinforcement percentages in two-choice procedures across a wide range of schedule values. The matching law not only provides mathematical predictions in choice situations but also provides a theoretical framework for accounting for choice behavior (Mazur, 1991). Second, the use of concurrent schedules also provided the opportunity to determine whether doses of drugs that are substituted for the training dose can produce effects outside the range of responding that was established on the two keys during training sessions. Under the usual schedules of reinforcement that maintain drug-discrimination responding, animals respond almost entirely on the drug key after drug and almost entirely on the vehicle key after vehicle. There is no opportunity to determine whether doses of the training drug that are higher than the training dose can produce more extreme responding on the drug key than the training dose does, because the animal is already responding 100% of the time on the drug key. However, under concurrent interval schedules, the distribution of responses on the two keys depends on the schedule values. This allows the investigator to use the schedule of reinforcement to determine the proportion of responses that will occur on the two keys and provides the opportunity for a greater proportion of responses to occur on the drug-biased key and a lower proportion of responses to occur on the saline-biased key during drug-substitution tests than occurs during training sessions.

In the present experiments, we continued our study of relative reinforcement of response alternatives in drug-discrimination experiments by using concurrent FI FI schedules to maintain responding. Concurrent FI FI schedules differ from the concurrent VI VI schedules used in our previous experiments (Snodgrass & McMillan, 1996) in that the time of reinforcer delivery under FI schedules has a temporal regularity that makes reinforcer delivery potentially more predictable than it is under VI schedules. In parallel with our previous research with these same birds on drug discrimination under the concurrent VI 60-s VI 240-s schedules (Snodgrass & Mc-Millan, 1996), the present study established drug discrimination under a concurrent FI 60-s FI 240-s schedule. Pentobarbital also served as the training drug in both studies. Other drugs used to determine the specificity of the pentobarbital stimulus were phencyclidine (PCP), chlordiazepoxide, ethanol, and methamphetamine. These drugs were used because they each produced different levels of substitution for the pentobarbital stimulus, and, excluding ethanol, the same drugs and doses had been used in our previous study of drug administration under concurrent VI VI schedules in these same birds (Snodgrass & McMillan, 1996).

METHOD

Subjects

Three male White Carneau pigeons (Palmetto Pigeon Plant), P257, P259, and P260, served as experimental subjects. These birds previously had been used for drug discrimination under concurrent VI VI schedules (Snodgrass & McMillan, 1996). They were individually housed with free access to food and water in a temperature- and humidity-controlled room that was maintained under a 12-hr normal phase lighting cycle. The pigeons had been maintained at 80% of their free-feeding weights in the previous experiments and continued to be maintained at these 80% weights for the duration of the current experiments.

Apparatus

The experimental chamber was a Gerbrands Model G5610 pigeon test cage enclosed in a Gerbrands Model G7211 soundand light-attenuating cubicle. Two 28-V DC lights illuminated the experimental chamber during the session, except during a food cycle when a light over the food hopper was illuminated. On the front panel of the cage three Gerbrands response keys (Model G7311) were mounted 7 cm apart, 20 cm above the grid floor. The center key was not used in these experiments and remained darkened at all times. When operative, the left key was blue and the right key was yellow. A force of 0.15 N or greater was required to operate these keys. A food hopper (Gerbrands) containing mixed grain was accessible to the pigeon for 4 s when scheduled contingencies were met. A desktop microcomputer, located in a room adjacent to the room containing the experimental chamber, controlled the schedule and recorded the data through a MED Associates interface.

Procedure

The methods for training these pigeons have been discussed in detail previously (Snodgrass & McMillan, 1996). Immediately following completion of the experiments using concurrent VI VI schedules (Snodgrass & McMillan, 1996), the schedule was changed to a concurrent FI 60-s FI 240-s schedule of reinforcement. Pigeons were trained to discriminate pentobarbital (5.0 mg/kg, i.m.) from saline under the concurrent FI 60-s FI 240-s schedule of reinforcement. Following an i.m. injection of 5.0 mg/kg pentobarbital or saline, birds were placed into the test chamber and a 10-min presession followed, during which all the lights in the chamber were extinguished and the keys were inoperative. After the presession time had elapsed, the houselights were illuminated, and the schedule contingencies were initiated. The training sessions terminated after the first reinforcer delivery that occurred after 60 min had elapsed.

Under the discrimination training procedure, both the left and right keys were transilluminated at session initiation, and an FI schedule was operative on each key. Thus, in each session, the pigeons were placed in a choice situation in which two response alternatives were available. Responses on each key were reinforced by 4-s access to mixed grain in the presence of each of the training stimuli each session, but the programmed rate of reinforcement differed by a ratio of 4:1. For Pigeon P257, the concurrent FI FI schedule was programmed to allow the bird to earn four times as many reinforcers on the right key (yellow key) compared to the number of reinforcers earned on the left key (blue key) after administration of the training drug. After vehicle administration, Pigeon P257 could earn four times as many reinforcers on the left key as could be earned on the right key. For Pigeons P259 and P260, the reinforcement contingencies after administration of the training drug and saline were the reverse of those for P257, so that the schedule during the training sessions was a concurrent FI 60-s FI 240-s or a concurrent FI 240-s FI 60-s schedule of reinforcement (hereafter it should be understood that the schedule values are in seconds and the abbreviation for seconds will be dropped from the schedule designation). Which of the concurrent schedules was in effect depended upon whether pentobarbital or saline had been administered before the session. Responding was maintained under these concurrent schedules for the duration of the study, with the exception of control and test sessions.

To limit reinforcement of switching between keys (Catania, 1966), a changeover delay (COD) of 3 s was imposed, such that a response could not produce a reinforcer unless it occurred at least 3 s after the bird had switched responding to a different key. Thus, an adventitious association between a changeover response and reinforcer delivery was minimized. Training sessions were conducted 6 days per week. During initial training, drug or saline was administered according to a double-alternation sequence, but later on, a single-alternation schedule of pentobarbital and saline administration (i.e., DSDSDS...) was employed. For discussion purposes, the key on which responses were reinforced under the FI 60 component after pentobarbital will be referred to as the pentobarbital-biased key, and the key on which responses were reinforced under the FI 60 component after saline will be referred to as the saline-biased

Test sessions began when the subjects reached the training criteria: The pigeons had to complete at least 51% of their responses on the key on which responses produced the reinforcer under the shorter FI component for 12 consecutive training sessions, six each of pentobarbital and saline. The percentage of responding on the appropriate key had to be within ±1 standard deviation of the mean of the previous six sessions. These criteria had to be met for both pentobarbital and saline administration prior to the initiation of substitution testing with other drug doses. These criteria were reached in all birds after 35 sessions of training. It should be noted that these birds already had considerable experience discriminating pentobarbital from saline under a concurrent VI VI schedule (Snodgrass & Mc-Millan, 1996), and it is presumed that it would have required many more sessions to meet these criteria had we initiated these experiments with new birds. Test sessions under the concurrent FI 150 FI 150 schedule were conducted on Tuesdays and Fridays, with training sessions under the concurrent FI 60 FI 240 schedule continuing on other days of the week. If a bird failed to reach criterion performance in a training session (less than 51% stimulus-appropriate responding), test sessions were postponed until these criteria had been met under both the pentobarbital and saline training conditions.

The procedure used during generalization tests was identical to the procedure used during training sessions, except that a concurrent FI 150 FI 150 schedule of reinforcement was in effect. This FI 150-s schedule value was chosen because it is intermediate between that of the 60-s FI and the 240-s FI values. The schedule also had the advantage that none of the pigeons had experienced this reinforcement rate during training sessions, so the reinforcement schedule was less likely to provide additional cues as to which response would be reinforced more frequently during the drug-substitution sessions. The pentobarbital and saline training doses were administered to the pigeons under the concurrent FI 150 FI 150 schedule prior to the administration of each dose-response curve and after all of the dose-response data had been collected. These sessions were designated as control sessions and measured the effect of the schedule change that was used during drugsubstitution tests on the stability of the stimulus control of behavior. Drug-substitution tests were conducted in single test sessions on different days for each dose for each pigeon. The training, control, and generalization test sessions were 40 min in duration, and data were collected for the entire session.

Finally, after dose–effect curves had been determined for all of the other test drugs that were substituted for pentobarbital, the pentobarbital dose–response curve was redetermined. During this redetermination, responses on each key were recorded separately by two cumulative recorders to permit a more detailed analysis of the relationship between patterns of responding on the two keys.

Data Analysis

The number of CODs, the number of responses and rate of responding under each FI component, time spent responding under each FI component (the first response at the beginning of the session began accumulating time on the FI component associated with the

key on which the response was made, and, thereafter, each time the pigeon switched keys, time accumulated for the other schedule component), and number of reinforcers earned under each schedule component were recorded. From these data the percentage of responding on the pentobarbital-biased key could be determined. The pentobarbital-biased key was defined as the key that was associated with the FI 60 component after the administration of pentobarbital during the training sessions. The saline-biased key was defined as the key that was associated with the FI 60 component after administration of saline during the training sessions. The percentage of responding on the pentobarbital-biased key and the percentage of time allotted to responding on the pentobarbital-biased key produced very similar data (see Appendix). If a pigeon earned less than half of the possible number of programmed reinforcers, the data obtained at that dose were not included in the analysis of dose-response effects.

Drugs

Pentobarbital sodium at doses of 1, 3, 5.6, 10, and 13 mg/kg (first determination of dose-response effects) or 3, 5, and 10 mg/kg (redetermination of pentobarbital effects with collection of cumulative response records) (Sigma Chemical Co.), phencyclidine hydrochloride (PCP) at doses of 0.1, 0.3, 0.56, and 1.0 mg/kg (National Institute on Drug Abuse), methamphetamine hydrochloride at doses of 0.3, 1.0, 1.8, 3.0, and 5.6 mg/kg (Sigma Chemical Co.), chlordiazepoxide hydrochloride at doses of 1.0, 3.0, 5.6, 7.8, and 10 mg/kg (Hoffman-La Roche, Inc.), and ethanol at doses of 0.25, 0.5, 0.75, 1.0, and 1.5 g/kg were studied. All drugs except ethanol were dissolved in 0.9% physiological saline to concentrations that allowed an injection volume of 1 ml/kg and were administered intramuscularly into a breast muscle. Physiological saline was also used for vehicle control injections. Doses are expressed as salts, except for ethanol.

Ethanol (100%) was diluted to a 10% weight/volume solution with tap water. The 10% ethanol solution or tap water, which was used as the vehicle control, was administered through a rubber tube that was passed down the esophagus into the proventriculus 15 min

Table 1

Means from six pentobarbital (Pb) training sessions and six saline (S) training sessions and the percentage of responding, reinforcers earned, and time allocated on the pentobarbital-biased key (%Pb) prior to the initiation of the testing phase in individual pigeons. The group means are also shown.

| | Responses | | |] | Reinforce | rs | Time | | | |
|---------------|----------------|---------|-----|----|-----------|-----|-------|-------|-----|--|
| Pigeon | Pb | S | %Pb | Pb | S | %Pb | Pb | S | %Pb | |
| Pentobarbit | al training se | essions | | | | | | | | |
| P257 | 3,120 | 546 | 85 | 37 | 8 | 83 | 1,896 | 333 | 85 | |
| P259 | 3,243 | 1,149 | 74 | 34 | 9 | 78 | 1,504 | 717 | 68 | |
| P260 | 2,392 | 519 | 82 | 36 | 9 | 80 | 1,745 | 471 | 79 | |
| M | 2,918 | 738 | 80 | 36 | 9 | 80 | 1,715 | 507 | 77 | |
| Saline traini | ing sessions | | | | | | | | | |
| P257 | 1,001 | 2,104 | 32 | 9 | 33 | 21 | 508 | 1,498 | 24 | |
| P259 | 1,064 | 2,121 | 33 | 9 | 36 | 20 | 605 | 1,614 | 27 | |
| P260 | 350 | 833 | 28 | 7 | 36 | 16 | 513 | 1,713 | 23 | |
| M | 805 | 1,686 | 31 | 8 | 35 | 19 | 542 | 1,608 | 25 | |

prior to session initiation. Doses for ethanol are expressed as grams per kilogram.

RESULTS

Table 1 shows the mean number of responses, the mean number of reinforcers earned, and the mean time allocated to responding on the pentobarbital-biased and saline-biased keys for each pigeon over the last six pentobarbital and the last six saline training sessions prior to the initiation of drug-substitution testing. During the pentobarbital training sessions, Pigeons P257 and P259 emitted a slightly higher total number of responses than during saline training sessions, whereas Pigeon P260 emitted considerably more responses during pentobarbital training sessions than during saline training sessions. However, the number of reinforcers obtained by each pigeon under the two training conditions was nearly identical. Thus, the training dose of pentobarbital did not suppress responding, nor did it decrease the number of reinforcers earned, compared to saline. After pentobarbital administration, the percentages of responses, time allocated to responding, and reinforcers obtained on the pentobarbital-biased key under the concurrent FI 60 FI 240 were close to the 80% predicted by the matching law. After saline administration, however, the percentages of responding and time allocation on the pentobarbital-biased key were slightly higher than the expected values (20%) compared with the percentage of reinforcers earned on the same key. Thus the birds undermatched responding under the saline training conditions. The number of CODs was similar for all 3 birds and did not differ for pentobarbital and saline training sessions (see Appendix).

Figure 1 shows the dose-effect curves for percentage of responding on the pentobarbital-biased key as a function of pentobarbital dose for both the initial determination of the pentobarbital dose-response curve and the redetermination of the effects of pentobarbital to provide cumulative response records, which was done at the end of the study. During the first determination of the pentobarbital dose-response curve, all birds showed increased responding on the drug-biased key as the dose of pentobarbital increased from 1.0 mg/kg to 5.6 mg/kg. For Pigeons P257 and P259, the peak of the dose-effect curve was reached at the 10 mg/kg dose, whereas for Pigeon P260, the peak occurred at a dose of 5.6 mg/kg. Perhaps of greater importance, at higher doses the curve descended for all birds, but especially for P260. During the second determination of the pentobarbital dose-response curve, for which a more limited range of doses was studied, the 3.0 mg/kg dose generated less responding on the drug-biased key for all 3 birds. The tendency for pentobarbital to be less potent in producing responding on the drug-biased key was also seen at the 5.0 and 10.0 mg/kg doses for Pigeon P259 but not for the other 2 birds. The 1.0 and 13.0 mg/kg doses of

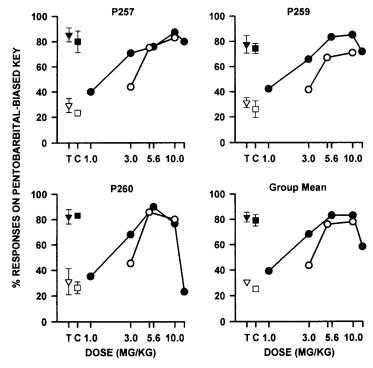


Fig. 1. The dose–response curve for the effects of pentobarbital on the percentage of responses on the key on which responses had been reinforced under the FI 60 component of the concurrent FI 60 FI 240 schedule after pentobarbital administration during training for Pigeons P257, P259, and P260 and the group mean. Abscissae: dose of pentobarbital (1, 3, 5, 5.6, 10, and 13 mg/kg). Ordinates: percentage of responses on pentobarbital-biased key. Brackets at T show ±1 standard deviation around the mean based on the data obtained during training sessions. Brackets at C show ±1 standard deviation around the mean based on the control sessions in which the schedule was changed to concurrent FI 150 FI 150, which was the schedule used during determination of the dose–response curves. The filled circles show the original pentobarbital dose–response curve, and the open circles show the redetermination of the effects of selected doses at the end of the study. The filled triangles and squares above T and C show the effects of saline injections during training and control sessions.

pentobarbital were not studied during the second determination of the pentobarbital dose–response curve.

Detailed data showing CODs, responses on each key, reinforcers earned on each key, and time allotted to responding on each key are shown for pentobarbital and the other drugs for each bird in the Appendix. There were no consistent effects on CODs with increasing doses of pentobarbital, although occasional decreases in CODs were observed for Pigeon P257 and increases in CODs for Pigeon P260.

Figure 2 shows the percentage of time spent responding on the pentobarbital-biased key as a function of pentobarbital dose. The percentages of time allocated to the pentobarbital-biased key resulted in dose–effect curves that were very similar to those based on the percentages of responses emitted on

the pentobarbital-biased key. For all pigeons, as the number of responses emitted on the pentobarbital-biased key increased or decreased, the amount of time allocated to responding on that key also increased or decreased. The dose–effect curves for percentage of time allotted to responding on the pentobarbital-biased key peaked and then descended after higher pentobarbital doses, just as occurred for the dose–effect curves for percentage of responses on the pentobarbital-biased key.

Figure 3 shows responses on the pentobarbital-biased key as a function of chlordiaze-poxide dose. Chlordiazepoxide caused a dose-dependent increase in the percentage of responses on the pentobarbital-biased key for Pigeons P257 and P259, whereas the dose-effect curve for P260 was more irregular. The

PENTOBARBITAL

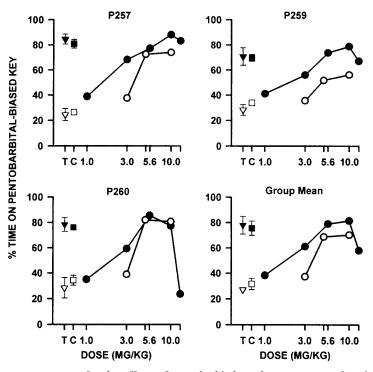


Fig. 2. The dose–response curve for the effects of pentobarbital on the percentage of session time allocated to responding on the key on which responses had been reinforced on the FI 60 component of the concurrent FI 60 FI 240 schedule after pentobarbital administration during training sessions. Abscissae: dose of pentobarbital (1, 3, 5, 5.6, 10, and 13 mg/kg). Ordinates: percentage of session time allocated to responding on the pentobarbital-biased key. Other details are as in Figure 1.

percentage of responding on the pentobarbital-biased key reached the levels attained under the pentobarbital training and control sessions. For P257, the peak in pentobarbitalbiased key responding occurred at the dose of 7.8 mg/kg chlordiazepoxide, and this bird failed to respond at the dose of 10.0 mg/kg; for P259, asymptotic responding occurred on the drug-biased key at the doses from 5.6 to 10.0 mg/kg; for P260, the peak effect occurred at the dose of 7.8 mg/kg, and there is a suggestion that at 10.0 mg/kg chlordiazepoxide the dose-response curve began to descend. Data for time allotted to responding on the drug-biased key were similar, except that the dose-response curve for P259 also began to descend after the highest dose (see Appendix). For Pigeons P257 and P259, there were decreases in CODs at two or more dose levels (see Appendix).

Ethanol dose–response data for percentage

of responses on the pentobarbital-biased key are shown in Figure 4. For Pigeon P257, with increasing doses there was a graded increase in the percentage of responses on the pentobarbital-biased key, and after the 1.5 g/kg dose of ethanol, P257 responded on the pentobarbital-biased key at the same percentages as occurred during pentobarbital training sessions. Pigeon P259 produced a similar ethanol dose-response curve, except for a small dip in the curve at the 1.0 g/kg dose. For Pigeon P260, there again was a suggestion that the dose-effect curve had risen to a peak and then began to descend after the highest dose of ethanol, although the decreases in the percentage of responses on the pentobarbital-biased key after the 1.0 and 1.5 g/kg doses were very small when compared to the 0.75 g/kg dose. The mean dose-response curve for ethanol was very similar to that for pentobarbital, except that the ethanol curve

CHLORDIAZEPOXIDE

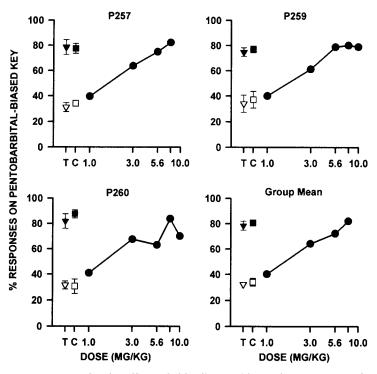


Fig. 3. The dose–response curve for the effects of chlordiazepoxide on the percentage of responses on the key on which responses had been reinforced under the FI 60 component of the concurrent FI 60 FI 240 schedule after pentobarbital administration during training sessions. Abscissae: dose of chlordiazepoxide (1.0, 3.0, 5.6, 7.8, and 10.0 mg/kg). Ordinates: percentage of responding on pentobarbital-biased key. Other details are as in Figure 1.

did not reach as high a peak nor did it begin to descend at the highest doses tested. Data for the time allocated to responding on the drug-biased key were similar to these data on percentage of responses on the drug key (see Appendix). CODs were decreased after several doses of ethanol for Pigeon P257 and after the highest dose for Pigeon P259, but Pigeon P260 showed increases in CODs after the two highest dose levels.

The PCP dose–response data are shown in Figure 5. For all 3 pigeons, the percentages of responding on the pentobarbital-biased key after the 0.1 mg/kg dose of PCP were approximately equal to the percentages under the training and control conditions after saline administration. Higher doses generally produced increasing responding on the pentobarbital-biased key, but the percentages of responding on the pentobarbital-biased key never reached the levels attained during pentobarbital training and control sessions. Thus,

the PCP dose–response curves did not reach the same asymptote as the pentobarbital dose–response curves, and the curves did not descend after the higher dose levels. When the time allotted to responding on the drugbiased key was measured, effects similar to those described for responding on the drugbiased key were obtained (see Appendix). Pigeons P257 and P259 showed decreases in CODs at the high doses of PCP (see Appendix).

Figure 6 shows the percentage of responding on the pentobarbital-biased key during the determination of the methamphetamine dose–response curve. When doses of methamphetamine were administered, all birds responded on the pentobarbital-biased key to about the same extent as they did under the training and control conditions after saline administration, although at some doses slightly more responding occurred on the pentobarbital-biased key than during saline train-

ETHANOL

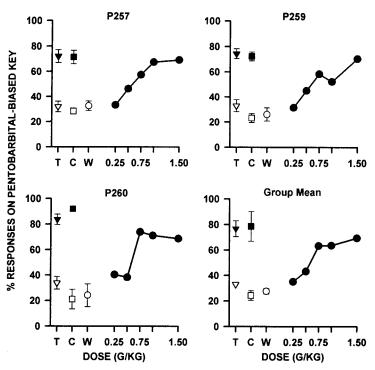


Fig. 4. The dose–response curve for the effects of ethanol on the percentage of responses on the key on which responses had been reinforced under the FI 60 component of the concurrent FI 60 FI 240 after pentobarbital administration during training sessions. Abscissae: dose of ethanol (0.25, 0.50, 0.75, 1.0, and 1.5 g/kg). Ordinates: percentage of responding on pentobarbital-biased key. Brackets at W represent ±1 standard deviation around the tap water control mean (open circles), which is based on five observations after tap water was administered down the esophagus into the proventriculus. Other details are as in Figure 1.

ing sessions. Again, similar effects were observed for time allotted to responding on the pentobarbital-biased key (see Appendix). Methamphetamine produced increases in CODs at low doses only in Pigeon P257.

Figure 7 shows the cumulative response records for all 3 birds during a training session following saline and 5.0 mg/kg pentobarbital. The cumulative records for the two components of the concurrent schedule have been overlaid for comparison. For all 3 birds after saline administration a typical pattern of responding appears to have developed under the FI 60 component (Ferster & Skinner, 1957, see p. 157), characterized by a pause after the delivery of the reinforcer and ending in a terminal rate of responding, which may or may not have been preceded by a brief period of positive acceleration in responding. Under the FI 240 component, re-

sponding is characterized by bursts of responding that look more typical of FR responding, followed by pauses. These bursts of responding are separated by periods of pausing that are longer than those seen under the FI 60 component of the schedule. Close examination of the relationship between the pattern of responding under the components of the concurrent schedule suggests that many of the bursts of responding under the FI 240 component occurred during the pauses under the FI 60 component. If reinforcer deliveries under the FI 60 component are compared with reinforcer deliveries under the FI 240 component, the bursts of responding after every fourth reinforcer delivery under the FI 60 component usually result in a reinforcer delivery under the FI 240 component. These relationships between component schedules hold in the same reg-

PHENCYCLIDINE

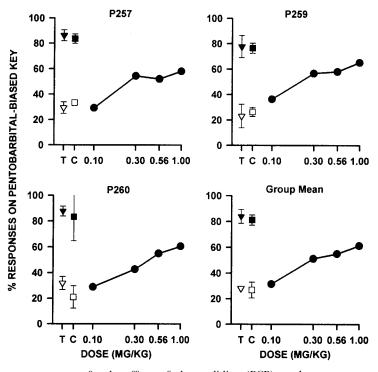


Fig. 5. The dose–response curve for the effects of phencyclidine (PCP) on the percentage of responses on the key on which responses had been reinforced under the FI 60 component of the concurrent FI 60 FI 240 schedule after pentobarbital administration during training sessions. Abscissae: dose of phencyclidine (0.1, 0.3, 0.56, and 1.0 mg/kg). Ordinates: percentage of responding on pentobarbital-biased key. Other details are as in Figure 1.

ular fashion regardless of whether saline or pentobarbital was administered before the training session.

It is difficult to quantify these relationships between FI components of the concurrent schedule because our computer program did not measure additional indices of FI performance and the cumulative records were available only for the second determination of the dose-response effects of pentobarbital. However, it was possible to measure the cumulative records in Figure 7 using a ruler to quantify the extent to which response bursts under the FI 240 component were correlated with postreinforcement pauses under the FI 60 component of the concurrent schedule. Response bursts under the FI 240 component of the concurrent schedule were defined as excursions of the cumulative response pen of greater than 0.1 mm (about five responses) without any obvious change in the slope of the line drawn by this pen. The number of these bursts of responses under FI 240 was totaled separately for each of the four FI 60 components that usually occurred during the FI 240 component. Then, using a ruler to align the cumulative records, the number of these bursts that occurred during the postreinforcement pause was determined and is reported as a percentage of the total number of bursts. These data are shown in Table 2.

Table 2 shows that bursts of responding under the FI 240 component were associated with postreinforcement pauses under the FI 60 component on an average of 88% of the time after saline and 81% of the time after pentobarbital. This association occurred in all birds for all four FI 60 components, except for the first FI 60 component after pentobarbital administration for P260 when only 44% of the bursts occurred during the postreinforcement pause on the key on which responses had been reinforced under the FI 60 component. These data suggest that the post-

METHAMPHETAMINE

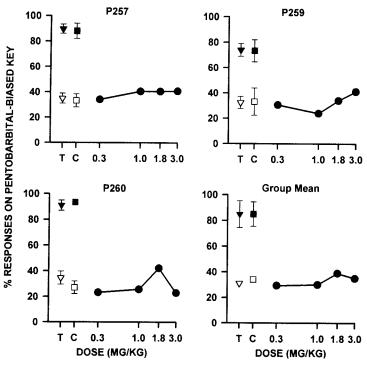


Fig. 6. The dose–response curve for the effects of methamphetamine on the percentage of responses on the key on which responses had been reinforced under the FI 60 component of the concurrent FI 60-s FI 240-s schedule after pentobarbital administration during training sessions. Abscissae: dose of methamphetamine (0.3, 1.0, 1.8, and 3.0 mg/kg). Ordinates: percentage of responding on pentobarbital-biased key. Other details as in Figure 1.

reinforcement pause under the FI 60 component set the occasion for response bursting under the longer FI component of the concurrent schedule.

During test sessions when other doses and other drugs were substituted for the training dose of pentobarbital, the schedule was changed to concurrent FI 150 FI 150 to prevent the pigeon from obtaining cues from the frequency of reinforcer delivery during these sessions. Figure 8 shows cumulative records from test sessions under concurrent FI 150 FI 150 with saline and the pentobarbital training dose administered before the session. Pigeon P257, after both saline and pentobarbital, continued to pause after food delivery and then to accelerate responding to a terminal rate that was maintained until delivery of the reinforcer on the key on which responses had previously produced the reinforcer under the FI 60 schedule component (left key after saline and right key after pentobarbital). However, as the session progressed, there was some tendency for this response pattern to begin to break down, especially after pentobarbital administration, when late in the session running and pausing began to appear on both response keys. Nevertheless, rates of responding remained considerably higher throughout the session on the key that had previously been associated with the shorter FI duration. Similar effects are seen in the records for P259, for which there is some tendency for the cumulative record to show response bursting on the key that had previously been associated with the shorter FI component (right key after saline and left key after pentobarbital). By late in the session, the rates on the two keys had almost equalized after pentobarbital administration. For Pigeon P260, FI responding was maintained at a much higher rate throughout the session on the key that had previously been associated with the shorter FI value following both

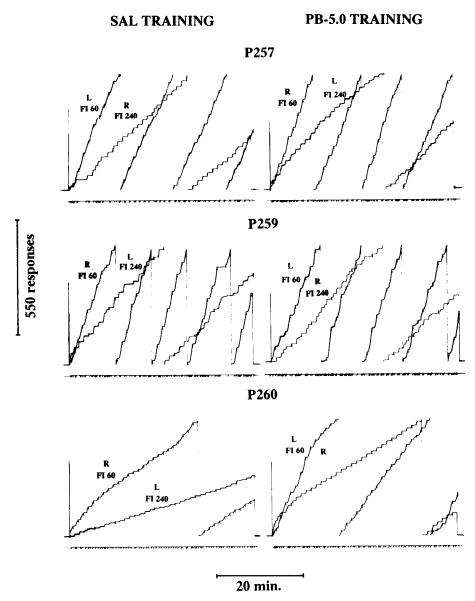


Fig. 7. Cumulative response records for individual animals during training sessions after administration of saline (left column) or 5.0 mg/kg pentobarbital (right column). Abscissae: time in minutes. Ordinates: cumulative responses. L and R indicate left and right keys, and the schedule under which responses were reinforced is indicated for each key. Hash marks on the horizontal line represent changeover responses when the animal switched from one key to the other. The cumulative records have been overlaid to permit comparison of patterns of responding on the two keys.

saline and the training dose of pentobarbital (right key after saline and left key after pentobarbital). For the last few FIs of the pentobarbital session, it appears that the response pattern seen at the beginning of the session began to change, with the pattern of

responding under both schedule components becoming more similar.

In Table 3, the number of bursts that occurred during the FI 150 component that had been programmed as the FI 240 component during training sessions is shown,

Table 2

Number of bursts under the FI 240 component for each of the four FI 60 components that occurred concurrently and the percentage of these bursts that occurred during the postreinforcement pause (PRP). Data from Figure 7.

| | | Sa | aline | Pento | barbital |
|------|----|--------|----------|--------|----------|
| Bird | FI | Bursts | % in PRP | Bursts | % in PRP |
| 257 | 1 | 11 | 64 | 9 | 67 |
| | 2 | 9 | 67 | 8 | 75 |
| | 3 | 8 | 75 | 10 | 90 |
| | 4 | 9 | 100 | 9 | 78 |
| 259 | 1 | 5 | 100 | 3 | 100 |
| | 2 | 8 | 100 | 10 | 100 |
| | 3 | 7 | 100 | 14 | 71 |
| | 4 | 8 | 63 | 9 | 67 |
| 260 | 1 | 1 | 100 | 9 | 44 |
| | 2 | 10 | 100 | 11 | 82 |
| | 3 | 9 | 100 | 9 | 100 |
| | 4 | 10 | 90 | 9 | 100 |
| M | | | 88 | | 81 |

along with the percentage of these bursts that occurred during the postreinforcement pause under the FI 150 component that had been programmed as the FI 60 component during training sessions. After saline administration, the birds continued to make most of their response bursts on the key that had previously been programmed as the FI 240 component during the postreinforcement pauses that occurred on the key that had previously been programmed as the FI 60 component, even though responding on both keys was reinforced under a concurrent FI 150 FI 150 schedule. This effect was most pronounced in Pigeon P260 and least in P257. After pentobarbital, there was less tendency for bursts of the FI 240 component to occur during the postreinforcement pauses on the key that had previously been programmed as the FI 60 component. For Pigeons P257 and P259 after pentobarbital administration, a majority of bursts of responses on the key that had previously been programmed as the FI 240 component were not associated with the postreinforcement pause on the other FI component.

Table 4 shows the number of reinforcers earned in each component of the concurrent FI 60 FI 240 and concurrent FI 150 FI 150 schedules (data from Figures 7 and 8). Under the concurrent FI 60 FI 240 schedule, the expected 4 to 1 ratio of reinforcers earned on the shorter FI component occurred. When

the schedule was changed to a concurrent FI 150 FI 150, the number of reinforcers earned on each schedule component became nearly equal.

In summary, responding on the key that had previously been associated with the shorter FI value continued to show a pause with an acceleration to a terminal rate during these test sessions under concurrent FI 150 FI 150. As the session progressed, there was a tendency for the temporal pattern of responding to begin to disintegrate, especially after pentobarbital. Nevertheless, the presence or absence of the drug usually produced more control over rate of responding than did the schedule change. Only late in the session after pentobarbital for Pigeon P259 did the rate on the key that had previously been associated with the longer FI value appear to approach the rate on the key with the shorter FI value.

Figures 9, 10, and 11 show cumulative records for saline and increasing doses of pentobarbital for individual birds. After saline, the typical test-day pattern developed for Pigeon P257 (Figure 9), with responding on the saline-biased key (key on which responses had been reinforced under the shorter FI duration after saline) showing a typical FI pattern and responding on the pentobarbital-biased key (key on which responses had been reinforced under the longer FI value after saline) showing the run-and-break pattern. These effects continued after the 3.0 mg/kg dose, except that the rate of responding on the pentobarbital-biased key increased slightly. After the 5.0 mg/kg dose, these effects were reversed, with the more typical FI pattern of responding appearing on the pentobarbital-biased key and the run-and-break pattern appearing on the saline-biased key. Toward the end of the session, there is evidence that the temporal control of responding on the pentobarbital-biased key was breaking down. After this dose there was considerably more responding on the pentobarbital-biased key than on the saline-biased key. Similar effects were obtained after the 10 mg/kg dose, except that the FI pattern of responding on the pentobarbital-biased key was well maintained throughout the session. Unfortunately, we did not redetermine the effects of the 13.0 mg/kg dose during the redetermination of the effects of pentobarbital,

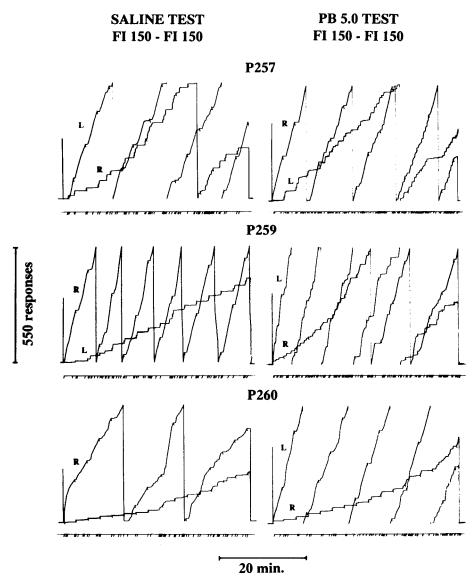


Fig. 8. Cumulative response records during control sessions when the schedule was changed from concurrent FI 60 FI 240 to FI 150 FI 150 on both response keys. Other details as in Figure 7.

so no cumulative records are available at the dose under which the curve began its descent (Figure 1).

Figure 10 shows the cumulative records for Pigeon P259 after saline and various doses of pentobarbital. As occurred with Pigeon P257, there was a gradual switch from the saline-biased key to the drug-biased key as the dose increased. A typical FI pattern of responding was characteristic of responding on the saline-biased key after administration of saline and the 3.0 mg/kg dose of pentobarbital, but

it began to disappear after 5.0 mg/kg pentobarbital and was replaced by run-and-break responding after the 10 mg/kg dose. The pattern of responding on the drug key showed some evidence of an FI pattern after the 5.0 mg/kg pentobarbital dose, but then changed to a pattern of short runs and pauses after the 10 mg/kg dose. Again, doses above 10 mg/kg were not administered when the effects of pentobarbital were redetermined.

Figure 11 shows similar cumulative records for Pigeon P260. As the dose of pentobarbital

Table 3

Number of bursts on the key previously programmed as the FI 240 component and percentage of those bursts that occurred during the postreinforcement pause (PRP) on the key previously programmed as the FI 60 component when the schedule was changed to the concurrent FI 150 FI 150. Data from Figure 8.

| | Sa | line | Pentobarbital | | |
|------|--------|-----------------|---------------|-----------------|--|
| Bird | Bursts | % during PRP | Bursts | % during PRP | |
| 257 | 37 | 57 | 44 | 36 | |
| 259 | 18 | 83 | 37 | 38 | |
| 260 | 14 | 93 | 27 | 63 | |

increased, responding on the saline-biased key decreased and responding on the pentobarbital-biased key increased. After saline administration, there were instances of runs and breaks in the cumulative records for the saline-biased key, although typical FI patterns of responding also occurred. Responding on the pentobarbital-biased key was characterized by relatively long pauses followed by a few responses, the last of which delivered the reinforcer. After the 3.0 mg/kg dose, responding on the pentobarbital-biased key was characterized by short runs either preceded or followed by breaks in responding, although some long runs occurred after the 3.0 mg/kg dose, especially early in the session. The pattern of responding on the saline-biased key was similar, except that the runs were more frequent. After the 5.0 and 10.0 mg/kg doses, the FI pattern of responding was seen on the pentobarbital-biased key and the run-and-break pattern had shifted to the saline key. Although the 13.0 mg/kg dose of pentobarbital was not studied in the redetermination of the pentobarbital dose-effect curve, it appears that the dose-response curve began to descend at 10 mg/kg (Figure 1 and Figure 11).

Figures 9, 10, and 11 also show that the increases in the dose of pentobarbital did not have major effects on mean overall rates of responding. The 10 mg/kg dose of pentobarbital reduced the overall rate of responding by about 20% compared to rates after saline for Pigeons P257 and P259, whereas the rate of responding for Pigeon P260 increased about 20%. These data are presented in further detail in the Appendix.

Table 4

Reinforcers earned on each key under concurrent FI 60 FI 240 and when the schedule was changed to concurrent FI 150 FI 150. Each column shows data for the same response key. Data from Figures 7 and 8.

| Bird | Sal | ine | Pentobarbital | | | |
|------|--------|--------|---------------|--------|--|--|
| | FI 60 | FI 240 | FI 60 | FI 240 | | |
| 257 | 36 | 8 | 36 | 9 | | |
| 259 | 35 | 9 | 34 | 8 | | |
| 260 | 36 | 8 | 36 | 9 | | |
| | FI 150 | FI 150 | FI 150 | FI 150 | | |
| 257 | 15 | 13 | 15 | 13 | | |
| 259 | 15 | 14 | 15 | 15 | | |
| 260 | 14 | 15 | 15 | 13 | | |

DISCUSSION

These studies extend our previous work on drug discrimination under concurrent VI VI schedules to concurrent FI FI schedules (Snodgrass & McMillan, 1996). In this extension, a pentobarbital discrimination was maintained under the behavioral contingencies of a concurrent FI 60 FI 240 schedule of reinforcement. Under concurrent FI FI schedules, matching occurs through the distribution of responses over both alternatives approximately in proportion to the frequency of reinforcement under the component schedules; however, the pattern of responding is different from that under concurrent VI VI schedules, because the interval between delivery of reinforcers under FI schedules remains constant as long as the animal continues to respond, thereby making the time of reinforcer delivery more predictable than it is under concurrent VI VI schedules.

The data from the present study using a concurrent FI FI schedule are in agreement with data from our previous drug-discrimination experiments with a concurrent VI VI schedule (Snodgrass & McMillan, 1996), both of which found that Herrnstein's matching law (Herrnstein, 1970, 1974) predicted the distribution of responses under concurrent interval schedules in drug-discrimination studies fairly well. The integration of drugdiscrimination data with the matching law offers several new opportunities. As Mazur (1991) has pointed out, there has been tremendous interest in using concurrent schedules to study choice behavior. A large database is available for comparing and

P257 TEST FI 150 - FI 150

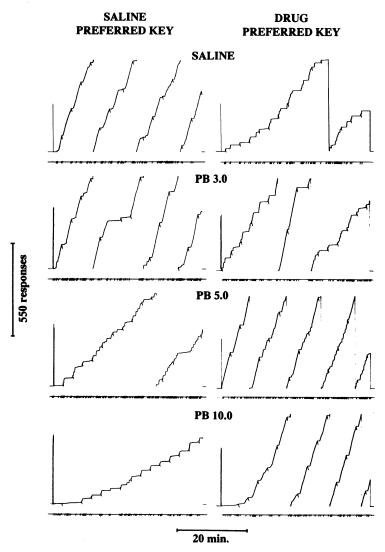


Fig. 9. Cumulative response records for Pigeon P257 during the second determination of the dose–effect curve for pentobarbital under the concurrent FI 150 FI 150 schedule. Responses on the key on which responses had been reinforced under the FI 60 component of the concurrent FI 60 FI 240 schedule after saline are shown in the left column and after 5.0 mg/kg pentobarbital in the right column. Abscissae: time in minutes. Ordinates: cumulative number of responses.

quantifying the effects of drugs with those of other variables on choice behavior. Furthermore, there have been a number of theoretical frameworks that have attempted to account for matching behavior (Herrnstein & Vaughan, 1980; Hinson & Staddon, 1983; Myerson & Miezin, 1980; Rachlin, Green, Kagel, & Battalio, 1976; Squires & Fantino, 1971; and others), some of which may be useful for the analysis of drug-discrimination behavior.

Analysis of the cumulative response records showed that the regularity of reinforcement under the shorter FI component of the concur-

P259

TEST FI 150 - FI 150

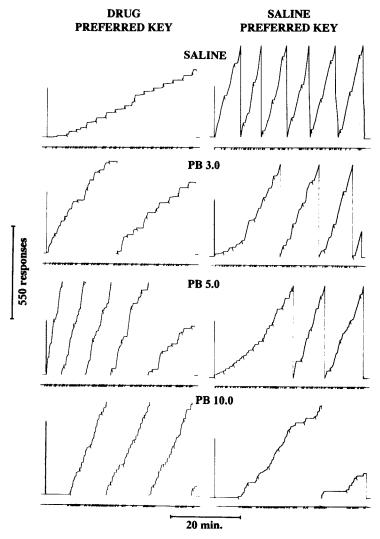


Fig. 10. Cumulative response records for Pigeon P259 during the second determination of the cumulative dose-response curve for pentobarbital under the concurrent FI 150 FI 150 schedule. Responses on the key on which responses had been reinforced under the FI 60 component of the concurrent FI 60 FI 240 schedule after saline are shown in the right column and after 5.0 mg/kg pentobarbital in the left column. Other details are as in Figure 9, but note that the columns are the reverse of Figure 9.

rent schedule largely controlled the pattern of responding under both schedule components. Under the FI 60 component of the schedule, a pattern of responding very similar to that described by Ferster and Skinner (1957) developed. At the beginning of the interval there was a pause in responding that was either followed by a short period of acceleration of re-

sponding to a terminal rate or a more abrupt transition from a pause to a terminal rate. During the pauses in responding under the FI 60 component, birds frequently responded with short high-rate bursts of responding on the key associated with the FI 240 component. Under the FI 240 component there was no indication of the usual pattern of fixed-interval respond-

P260 TEST FI 150 - FI 150

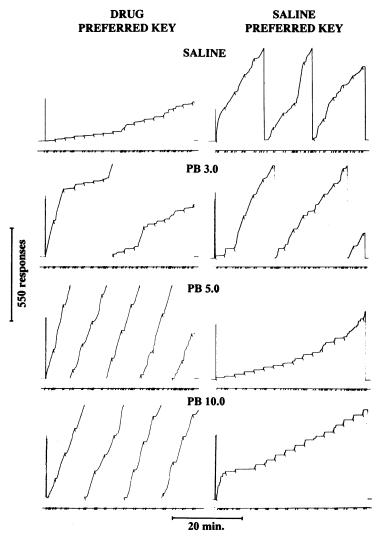


Fig. 11. Cumulative response records for Pigeon P260 during the second determination of the cumulative dose-response curve for pentobarbital under the concurrent FI 150 FI 150 schedule. Details as in Figure 10.

ing; rather, a run-and-break pattern of responding was observed. Although we could not find other examples of patterns of responding under concurrent FI FI schedules in the literature, this pattern of responding under concurrent FI FI schedules was predicted by Catania (1966), who suggested that when there is a consistent relationship between FI components of a concurrent schedule (e.g., when one FI component is a simple multiple of the other),

reinforcement programmed by one schedule would come to be a discriminative stimulus for a changeover to the other schedule. These data suggest that responding under the two components of the concurrent FI FI schedule were not independent. It appears that periods of pausing after delivery of the reinforcer under the shorter FI component set the occasion for responding on the longer FI component.

Nevertheless, this combination of an FI pat-

tern of responding on one key and run-andbreak responding on the other resulted in the percentages of responding on the two keys close to those predicted by the matching law (Davison & McCarthy, 1988; Herrnstein, 1970, 1974). As shown in Table 1 during the pentobarbital training sessions, percentage of responding on the pentobarbital-biased key, percentage of reinforcers earned on the pentobarbital-biased key, and time spent responding on the pentobarbital-biased key under the concurrent FI 60 FI 240 were very close to the 80% predicted by the matching law. During saline training sessions, the pigeons responded slightly less often on the saline key (an average of 69%) and spent less time responding on that key (an average of 75%) than the 80% predicted by the matching law; however, the percentage of reinforcers earned on the saline key was close to the value predicted by the matching law for 2 of the 3 birds and was fairly close for Pigeon P260. A slight degree of undermatching has been previously reported for responding under concurrent VI VI schedules (Baum, 1979).

During the test sessions, the concurrent FI 60 FI 240 schedule was changed to a concurrent FI 150 FI 150 schedule. The schedule change was made so that when drug-substitution tests were conducted, the schedule would be different on both keys from the schedule during training sessions. By using a different reinforcement schedule during drug-substitution tests than that used during training, the possibility that the bird's behavior would be controlled completely by the schedule rather than by the drug should be decreased. However, when this was done, it became necessary to determine whether the change in reinforcement contingencies would disrupt stimulus control by training doses of the training drug. If the drug or saline stimulus failed to control the responding of the well-trained pigeons when the schedule was changed to concurrent FI 150 FI 150 during such test sessions, the percentages of responding should have approximated 50% on each key. This did not occur. The relative percentages of responding on the two keys remained appropriate for the concurrent FI 60 FI 240 training schedule. Not only did the relative rate of responding remain appropriate for the concurrent FI 60 FI 240 schedule, but the pattern of responding also remained similar for most of the session. On the key that had previously been associated with the FI 60 component of the schedule, a typical FI pattern of responding continued to occur under the FI 150 component that was now associated with that key, despite the lengthening of the interval. On the key that had previously been associated with the FI 240 component of the schedule, the run-andbreak pattern continued to be observed. However, the terminal response rate on the key that had previously been associated with the FI 60 component continued over a longer duration because delivery of the reinforcer was delayed by the longer interval under the FI 150 component. Similarly, the pauses in responding on the key that had previously been associated with the FI 240 component also lasted longer because of the sustained FI responding on the other key. This is a powerful demonstration of the interrelationship between these two components of the concurrent FI FI schedule. Late in the session there was some indication that these relationships were becoming unstable after pentobarbital administration, although less so after saline administration. This instability, as shown by a breakdown of the patterns of responding described above, may have occurred because late in the session the consequences of the change in reinforcer frequency started to exert control over responding to disrupt the previous pattern of responding. Because this disruption of responding occurred late in the session, it produced minimal changes in the percentages of responding on the two keys. Alternatively, instability may have occurred because the pentobarbital stimulus may have been weakening late in the session due to falling blood levels of the drug. This possibility is attractive because the effect was much less pronounced after saline administration when falling blood levels would not be a factor; however, there was no evidence that the pentobarbital stimulus was weakening late in pentobarbital training sessions, so this explanation does not account for the data. Perhaps both the schedule change and a decrease in pentobarbital blood levels late in the session contributed to the loss of the pattern of responding that was observed earlier in the ses-

When pentobarbital dose-response curves

were determined, the patterns of responding described above could be observed in the cumulative records. After 3.0 mg/kg pentobarbital administration, a typical pause followed by a rapid acceleration to a terminal rate occurred on the key on which responses had been reinforced under the FI 60 component after saline administration during training sessions, and run-and-break responding occurred on the other key. At the two higher doses, similar effects were observed, except that the FI pattern of responding was now associated with the key on which responses had been reinforced under the FI 60 component after pentobarbital administration during training sessions, and the run-andbreak pattern now occurred on the other key. Thus the pattern of responding on the two keys could usually be described as either being "saline-like" or "pentobarbital-like" at a given dose for each bird (Pigeon P259 was an exception following 10 mg/kg pentobarbital, when run-and-break responding tended to occur on both keys).

Although these somewhat qualitative differences in response pattern occurred as the dose of pentobarbital increased, there were also obvious quantitative differences. As the dose of pentobarbital increased, the percentage of responses on the drug key increased for each subject until the curve reached a maximum. Thus, the dose-response curves were graded rather than quantal. This result is similar to our finding using concurrent VI VI schedules (Snodgrass & McMillan, 1996). Other investigators (Holloway & Gauvin, 1989; Stolerman, 1991; Young, 1991) have emphasized the importance of the schedule of reinforcement in determining whether responding in drug-discrimination experiments is nominal or continuous. Under the FR drug-discrimination procedure described by Colpaert (1987), the form of the dose-response curve is quantal because responding in individual animals is nominal. Under the concurrent FI FI schedule procedure of the present study and the VI VI schedule in our previous study, the dose-response curves were graded because response rates in individual animals varied continuously.

We have previously discussed some of the implications of graded verses quantal doseresponse curves in drug-discrimination studies (Snodgrass & McMillan, 1996). Colpaert

(1986) and Stolerman (1991) have also emphasized the importance of this question. If dose-response curves are continuous, it suggests that there is a continuum of stimulus control produced across different doses of drug. It is possible that subjects respond to stimuli in either a quantal or graded manner, depending on the consequences (the schedule of reinforcement) that result from such patterns of responding. According to this idea, subjects would respond to graded differences in stimuli under interval schedules by responding in graded fashion and would respond to the presence or absence of stimuli under ratio schedules by responding nominally to maximize reinforcement, as predicted by the matching law.

When the animals matched the frequency of responding to the frequency of reinforcer delivery programmed under the concurrent FI 60 FI 240 schedule during training sessions after pentobarbital administration, about 80% of the responses occurred on the drug key and about 30% occurred on the saline key. This nonexclusive pattern of responding makes it possible for dose-effect curves to start below and end above the values observed during training sessions (e.g., <30% and >80%). In most drug-discrimination studies, during training sessions well-trained animals respond at near 100% on the drug key after drug administration and at near 0% on the drug key after vehicle administration. When generalization curves are determined, animals cannot respond outside the range of responding seen after administration of saline (0%) or the training drug (100%). It has been suggested that the data compression caused by these ceiling and floor effects is one of the factors that limits measurement of drug-discrimination data to ordinal scales (Stolerman, 1991). The use of concurrent schedules at least opens the possibility that more extreme responses to a drug can be observed than occurred during training, because the concurrent schedule produces responding on the drug-biased key that is less than 100% and produces responding on the saline-biased key that is greater than 0%. Using concurrent schedules, it may be possible to determine whether drugs can produce stimuli on the same quantitative dimension as the training drug but at a greater intensity than the training drug. Snodgrass and McMillan (1996) provided some evidence that high doses of pentobarbital can produce more responding on the drug key than does the training dose of pentobarbital when the responding of pigeons is maintained under a concurrent VI 60 VI 260 schedule. In that study, 1 pigeon (P257) responded considerably more often on the drug-biased key after high doses of pentobarbital (second determination of pentobarbital effects) than during training sessions after pentobarbital, and another subject (P260) responded less often on the saline key after 3.0 mg/kg methamphetamine than during training sessions after saline administration. Such effects were not observed in the present study. For Pigeon P257 and perhaps for Pigeon P259, the peak of the dose-effect curve occurred at 10 mg/kg, a dose higher than the 5.0 mg/kg training dose. However, the pentobarbital dose-effect curve did not ascend beyond the levels that were obtained with the training dose; in fact, the pentobarbital dose-effect curve turned over and began to descend after higher doses of pentobarbital in all 3 birds, but especially for Pigeon P260. The descent of the dose-response curve might occur because at doses of pentobarbital higher than the training dose the drug produces stimuli that are weaker than the training dose, which seems unlikely. Another possibility is that doses of pentobarbital higher than the training dose produce qualitatively different stimulus effects that either block or replace the stimulus effects of the training dose. We do not know why the pentobarbital dose-effect curve descended in our studies with the concurrent FI 60 FI 240 schedule but not in the same birds with responding maintained under a concurrent VI 60 VI 240 schedule (Snodgrass & McMillan, 1996), although it should be noted that in the previous study the 13.0 mg/kg dose of pentobarbital eliminated responding in 2 of the 3 birds. The 13.0 mg/kg dose is the same dose under which the dose-response curve began to descend in the present study. Perhaps if responding had occurred after the 13.0 mg/kg dose in the previous study using the concurrent VI VI schedule, the pentobarbital doseeffect curve would also have begun to descend after high doses in that study.

As anticipated, chlordiazepoxide substituted completely for pentobarbital in all birds,

as has been reported using other procedures in other species (Barry & Krimmer, 1978). There was less tendency for the chlordiazepoxide curve to show a descending leg at high doses, although there was a suggestion of this effect in Pigeon P260 and to a lesser extent in P259. Ethanol also substituted for pentobarbital, although the substitution was not quite complete for Pigeon P260. Ethanol has also been reported to substitute for pentobarbital in animals trained to discriminate pentobarbital from no drug (Overton, 1977). Phencyclidine produced only partial substitution for pentobarbital in all 3 birds. Phencyclidine has been reported to produce a range of degrees of substitution for pentobarbital in other studies (Snodgrass & Mc-Millan, 1991, 1996; Willetts & Balster, 1989). All of these drugs produced graded effects in individual animals. In contrast, methamphetamine did not substitute for pentobarbital in these experiments, a common finding in the literature (Snodgrass & McMillan, 1996). Thus, in drug-substitution tests, the concurrent FI schedule produces effects that are very similar to those observed in traditional drug-discrimination procedures. Like the concurrent VI VI schedule, the concurrent FI FI schedule offers several advantages over traditional schedules that have been used in drug-discrimination studies, including the opportunity to determine whether drugs can produce responding outside the range of effects seen during training sessions, the generation of graded dose-effect curves in individual animals, and the opportunity to integrate drug-discrimination data with the matching law. The concurrent FI FI schedule may offer advantages over the concurrent VI VI schedule in that it produces different patterns of responding on the two keys (run and break vs. a more typical FI pattern) that switch from the saline-biased key to the drugbiased key as the dose of the training drug increases.

REFERENCES

Barry, H., III, & Krimmer, E. C. (1978). Similarities and differences in discriminative stimulus effects of chlordiazepoxide, pentobarbital, ethanol, and other sedatives. In F. C. Colpaert & J. A. Rosecrans (Eds.), Stimulus properties of drugs: Ten years of progress (pp. 31–51). Amsterdam: Elsevier.

Baum, W. M. (1979). Matching, undermatching, and

- overmatching in studies of choice. Journal of the Experimental Analysis of Behavior, 32, 269–281.
- Catania, A. C. (1966). Concurrent operants. In W. K. Honig (Ed.), Operant behavior: Areas of research and application (pp. 213–270). New York: Appleton-Century-Crofts.
- Colpaert, F. C. (1986). Drug discrimination: Behavioral, pharmacological and molecular mechanisms of discriminative drug effects. In S. R. Goldberg & I. P. Stolerman (Eds.), Behavioral analysis of drug dependence (pp. 161–193). Orlando, FL: Academic Press.
- Colpaert, F. C. (1987). Drug discrimination: Methods of manipulation, measurement and analysis. In M. A. Bozarth (Ed.), Methods of assessing the reinforcing property of abused drugs (pp. 341–372). New York: Springer-Verlag.
- Davison, M. C., & McCarthy, D. (1988). *The matching law:* A research review. Hillsdale, NJ: Erlbaum.
- Ferster, C. B., & Skinner, B. F. (1957). Schedules of reinforcement. New York: Appleton-Century-Crofts.
- Gouvier, W. D., Akins, F. R., & Trapold, M. A. (1984). Assessment of drug state dimensionally via drug-drug training and stimulus generalization testing. *Pharma-cology Biochemistry and Behavior*, 24, 687–693.
- Herrnstein, R. J. (1970). On the law of effect. *Journal of the Experimental Analysis of Behavior, 13,* 243–266.
- Herrnstein, R. J. (1974). Formal properties of the matching law. Journal of the Experimental Analysis of Behavior, 21, 159–164.
- Herrnstein, R. J., & Vaughan, W. (1980). Melioration and behavioral allocation. In J. E. R. Staddon (Ed.), Limits to action: The allocation of individual behavior (pp. 143–176). New York: Academic Press.
- Hinson, J. M., & Staddon, J. E. R. (1983). Hill climbing by pigeons. *Journal of the Experimental Analysis of Behav*ior, 39, 25–47.
- Holloway, F. A., & Gauvin, D. V. (1989). Comments on method and theory in drug discrimination: A potpourri of problems, perplexities and possibilities. *Drug Development Research*, 16, 195–207.
- Kelleher, R. T., & Morse, W. H. (1964). Escape behavior and punished behavior. Federation Proceedings, 23, 808– 817
- Koek, W., & Slangen, J. L. (1982). Effects of reinforcement differences between drug and saline sessions on discriminative stimulus properties of fentanyl. In F. C. Colpaert & J. L. Slangen (Eds.), *Drug discrimination applications in CNS pharmacology* (pp. 343–354). Amsterdam: Elsevier.
- Krimmer, E. C., McGuire, M. S., & Barry, H., III. (1984).
 Effects of the training dose on generalization of morphine stimulus to clonidine. *Pharmacology Biochemistry and Behavior*, 20, 669–673.
- Massey, B. W., McMillan, D. E., & Wessinger, W. D. (1992). Discriminative-stimulus control by morphine in the pigeon under a fixed-interval schedule of reinforcement. *Behavioural Pharmacology*, 3, 475–488.
- Mathis, D. A., & Emmett-Oglesby, M. E. (1990). Quantal

- vs. graded generalization in drug discrimination: Measuring a graded response. *Journal of Neuroscience Methods*, *31*, 23–33.
- Mazur, J. E. (1991). Choice. In I. H. Iversen & K. Lattal (Eds.), *Experimental analysis of behavior* (Part I, pp. 219–250). New York: Elsevier.
- McMillan, D. E., Cole-Fullenwider, D. A., Hardwick, W. C., & Wenger, G. R. (1982). Phencyclidine discrimination in the pigeon using color tracking under second-order schedules. *Journal of the Experimental Analysis of Behavior, 37*, 143–147.
- McMillan, D. E., & Hardwick, W. C. (1996). Pentobarbital discrimination and generalization to other drugs under multiple fixed-ratio fixed-interval schedules. Behavioural Pharmacology, 65, 495–512.
- McMillan, D. E., & Wenger, G. R. (1984). Bias of phencyclidine discrimination by the schedule of reinforcement. *Journal of the Experimental Analysis of Behavior*, 42, 51–66.
- Myerson, J., & Miezin, F. M. (1980). The kinetics of choice: An operant systems analysis. *Psychology Review*, 87, 160–174.
- Overton, D. A. (1977). Comparison of ethanol, pentobarbital, and phenobarbital using drug vs. drug discrimination training. *Psychopharmacology*, 53, 195–199.
- Rachlin, H. L., Green, L., Kagel, J. H., & Battalio, R. C. (1976). Economic demand theory and psychological studies of choice. In G. H. Bower (Ed.), *The psychology* of learning and motivation (Vol. 10, pp. 129–154). New York: Academic Press.
- Snodgrass, S. H., & McMillan, D. E. (1991). Effects of schedule of reinforcement on a pentobarbital discrimination in rats. *Journal of the Experimental Analysis* of Behavior, 56, 313–329.
- Snodgrass, S. H., & McMillan, D. E. (1996). Drug discrimination under concurrent schedules. *Journal of the* Experimental Analysis of Behavior, 65, 495–512.
- Squires, N., & Fantino, E. (1971). A model for choice in simple concurrent and concurrent-chain schedules. Journal of the Experimental Analysis of Behavior, 15, 27– 38.
- Stolerman, I. P. (1991). Measures of stimulus generalization in drug discrimination experiments. *Behavioural Pharmacology*, 2, 265–282.
- Willetts, J., & Balster, R. L. (1989). Pentobarbital-like stimulus effects of N-methyl-D-aspartate antagonists. Journal of Pharmacology and Experimental Therapeutics, 249, 438–443.
- Witkin, J. M., Carter, R. B., & Dykstra, L. A. (1980). Discriminative stimulus properties of d-amphetaminepentobarbital combinations. *Psychopharmacology*, 68, 269–276.
- Young, A. M. (1991). The time is ripe for an experimental analysis of measurement issues. *Behavioural Pharmacology*, 2, 287–291.

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APPENDIX

For each pigeon, the dose–response data for each drug are shown. These data are the number of changeover delays (CODs), the number of responses, reinforcers, and amount of time (seconds) allocated to the pentobarbital (Pb) and saline (S) biased keys, and the percentage of responses and time emitted on the pentobarbital-biased key (%Pb).

| | | | Responses | | | Reinforcers | | Time | | |
|------------|------------|--------|-----------|-------|-----|-------------|----|-------|-------|-----|
| Bird | Dose | CODs | Pb | S | %Pb | Pb | S | Pb | S | %Pb |
| Pentobarb | ital (mg/k | (g) | | | | | | | | |
| P257 | 0.0 | 169 | 878 | 2,968 | 23 | 14 | 15 | 730 | 2,050 | 26 |
| | 1.0 | 126 | 1,241 | 1,868 | 40 | 14 | 14 | 887 | 1,396 | 39 |
| | 3.0 | 150 | 2,709 | 1,117 | 71 | 15 | 13 | 1,559 | 726 | 68 |
| | 5.6 | 164 | 2,805 | 892 | 76 | 15 | 13 | 1,764 | 517 | 77 |
| | 10.0 | 118 | 1,996 | 292 | 87 | 14 | 10 | 2,033 | 275 | 88 |
| | 13.0 | 141 | 2,604 | 657 | 80 | 11 | 15 | 1,906 | 386 | 83 |
| P259 | 0.0 | 159 | 1,068 | 3,157 | 25 | 14 | 16 | 806 | 1,537 | 34 |
| | 1.0 | 172 | 1,522 | 2,075 | 42 | 14 | 15 | 1,015 | 1,459 | 41 |
| | 3.0 | 146 | 3,032 | 1,575 | 66 | 14 | 15 | 1,274 | 1,004 | 56 |
| | 5.6 | 95 | 3,717 | 734 | 84 | 15 | 14 | 1,681 | 597 | 74 |
| | 10.0 | 110 | 1,476 | 255 | 85 | 14 | 12 | 1,525 | 412 | 79 |
| | 13.0 | 125 | 3,874 | 1,504 | 72 | 15 | 15 | 1,523 | 747 | 67 |
| P260 | 0.0 | 90 | 495 | 1,437 | 25 | 14 | 16 | 795 | 1,520 | 34 |
| | 1.0 | 67 | 515 | 947 | 35 | 13 | 15 | 799 | 1,484 | 35 |
| | 3.0 | 80 | 1,551 | 727 | 68 | 13 | 13 | 1,360 | 933 | 59 |
| | 5.6 | 48 | 1,967 | 220 | 90 | 15 | 15 | 1,947 | 329 | 86 |
| | 10.0 | 107 | 1,486 | 452 | 77 | 15 | 14 | 1,382 | 406 | 77 |
| | 13.0 | 160 | 533 | 1,766 | 23 | 10 | 16 | 545 | 1,749 | 24 |
| Phencyclid | line (mg/l | kg) | | | | | | | | |
| P257 | 0.0 | 142 | 1,189 | 2,394 | 33 | 14 | 13 | 685 | 1,598 | 30 |
| 1 437 | 1.0 | 101 | 931 | 2,266 | 29 | 12 | 14 | 771 | 1,520 | 34 |
| | 0.3 | 180 | 2,666 | 2,238 | 54 | 14 | 13 | 1,198 | 1,082 | 53 |
| | 0.56 | 77 | 1,874 | 1,725 | 52 | 15 | 14 | 1,306 | 973 | 57 |
| | 1.0 | 70 | 1,814 | 1,308 | 58 | 15 | 13 | 1,332 | 952 | 58 |
| P259 | 0.0 | 192 | 1,129 | 3,164 | 26 | 14 | 16 | 760 | 1,514 | 33 |
| 1200 | 0.1 | 166 | 1,413 | 2,478 | 36 | 13 | 15 | 724 | 1,557 | 32 |
| | 0.3 | 128 | 2,610 | 1,992 | 57 | 14 | 15 | 1,138 | 1,139 | 50 |
| | 0.56 | 152 | 2,200 | 1,596 | 58 | 14 | 14 | 1,265 | 1,133 | 55 |
| | 1.0 | 86 | 937 | 500 | 65 | 12 | 10 | 1,490 | 828 | 64 |
| P260 | 0.0 | 78 | 254 | 950 | 21 | 15 | 16 | 652 | 1,622 | 29 |
| 1 200 | 0.1 | 51 | 295 | 727 | 29 | 13 | 15 | 747 | 1,537 | 33 |
| | 0.3 | 49 | 575 | 771 | 43 | 15 | 15 | 766 | 1,509 | 34 |
| | 0.56 | 71 | 1,870 | 1,531 | 55 | 15 | 14 | 1,331 | 982 | 58 |
| | 1.0 | 51 | 613 | 399 | 61 | 14 | 10 | 1,494 | 827 | 64 |
| Methamph | netamine (| mg/kg) | | | | | | , | | |
| P257 | 0.0 | 163 | 1,010 | 2,015 | 33 | 15 | 14 | 835 | 1,440 | 37 |
| 1 437 | 0.3 | 208 | 1,027 | 1,978 | 34 | 14 | 14 | 989 | 1,290 | 43 |
| | 1.0 | 189 | 1,364 | 2,004 | 41 | 14 | 15 | 773 | 1,507 | 34 |
| | 1.8 | 168 | 1,296 | 1,903 | 41 | 16 | 14 | 899 | 1,307 | 40 |
| | 3.0 | 134 | 1,134 | 1,644 | 41 | 14 | 15 | 893 | 1,383 | 39 |
| P259 | 0.0 | 189 | 1,218 | 2,545 | 32 | 14 | 16 | 737 | 1,537 | 32 |
| 1 433 | 0.3 | 167 | 1,580 | 3,580 | 31 | 13 | 16 | 704 | 1,557 | 31 |
| | 1.0 | 146 | 1,233 | 3,906 | 24 | 13 | 16 | 550 | 1,727 | 24 |
| | 1.8 | 165 | 1,511 | 2,914 | 34 | 14 | 15 | 739 | 1,535 | 33 |
| | 3.0 | 157 | 1,664 | 2,370 | 41 | 13 | 15 | 689 | 1,588 | 30 |
| | 5.6 | 109 | 651 | 1,082 | 38 | 9 | 10 | 851 | 1,366 | 37 |
| P260 | 0.0 | 44 | 369 | 977 | 27 | 15 | 16 | 573 | 1,681 | 25 |
| 1 400 | 0.3 | 43 | 330 | 1,086 | 23 | 15 | 16 | 509 | 1,763 | 22 |
| | 1.0 | 55 | 325 | 938 | 26 | 15 | 16 | 591 | 1,630 | 27 |
| | 1.8 | 36 | 337 | 460 | 42 | 13 | 11 | 959 | 1,344 | 42 |
| | 3.0 | 41 | 140 | 469 | 23 | 10 | 14 | 328 | 2,011 | 14 |

APPENDIX

(Continued)

| | | | 1 | Responses | | Reinf | orcers | Time | | |
|------------|------------|-----------|-------------|-------------|--------|-------|--------|-------|-------|-----|
| Bird | Dose | CODs | Pb | S | %Pb | Pb | S | Pb | S | %Pb |
| Chlordiaze | epoxide (n | ng/kg) | | | | | | | | |
| P257 | 0.0 | 154 | 1,133 | 2,194 | 34 | 15 | 14 | 774 | 1,502 | 34 |
| | 1.0 | 96 | 1,371 | 2,093 | 40 | 13 | 15 | 849 | 1,435 | 37 |
| | 3.0 | 82 | 1,455 | 829 | 64 | 15 | 13 | 1,657 | 627 | 73 |
| | 5.6 | 96 | 1,230 | 411 | 75 | 15 | 10 | 1,990 | 548 | 78 |
| | 7.8 | 95 | 1,895 | 410 | 82 | 15 | 10 | 2,091 | 540 | 80 |
| P259 | 0.0 | 163 | 1,534 | 2,611 | 37 | 14 | 15 | 799 | 1,473 | 35 |
| | 1.0 | 152 | 1,660 | 2,483 | 40 | 14 | 15 | 708 | 1,267 | 36 |
| | 3.0 | 146 | 2,743 | 1,730 | 61 | 14 | 15 | 1,211 | 1,065 | 53 |
| | 5.6 | 83 | 2,326 | 620 | 79 | 11 | 10 | 1,781 | 531 | 77 |
| | 7.8 | 46 | 1,254 | 309 | 80 | 10 | 10 | 2,128 | 237 | 90 |
| | 10.0 | 100 | 3,271 | 864 | 79 | 13 | 12 | 1,653 | 641 | 72 |
| P260 | 0.0 | 31 | 309 | 698 | 31 | 15 | 15 | 804 | 1,474 | 35 |
| | 1.0 | 30 | 451 | 651 | 41 | 14 | 15 | 946 | 1,835 | 34 |
| | 3.0 | 40 | 1,878 | 903 | 68 | 15 | 15 | 1,741 | 535 | 76 |
| | 5.6 | 60 | 1,091 | 639 | 63 | 14 | 14 | 1,524 | 765 | 67 |
| | 7.8 | 48 | 1,730 | 335 | 84 | 15 | 14 | 1,766 | 516 | 77 |
| | 10.0 | 81 | 1,008 | 430 | 70 | 12 | 11 | 1,633 | 669 | 71 |
| Ethanol (g | (/kg) | | | | | | | | | |
| P257 | 0.00 | 135 | 968 | 1,970 | 33 | 14 | 14 | 757 | 1,504 | 33 |
| 120, | 0.25 | 98 | 1,197 | 2,388 | 33 | 14 | 14 | 733 | 1,549 | 32 |
| | 0.50 | 72 | 1,294 | 1,505 | 46 | 14 | 13 | 1,236 | 1,050 | 54 |
| | 0.75 | 132 | 1,742 | 1,293 | 57 | 14 | 14 | 1,427 | 858 | 62 |
| | 1.00 | 114 | 1,908 | 923 | 67 | 15 | 13 | 1,613 | 673 | 71 |
| | 1.50 | 72 | 1,418 | 633 | 69 | 13 | 13 | 1,452 | 841 | 63 |
| P259 | 0.00 | 100 | 1,022 | 3,002 | 26 | 14 | 16 | 647 | 1,626 | 28 |
| | 0.25 | 88 | 1,473 | 3,208 | 31 | 13 | 16 | 654 | 1,625 | 29 |
| | 0.50 | 119 | 2,045 | 2,492 | 45 | 15 | 16 | 1,000 | 1,269 | 44 |
| | 0.75 | 121 | 2,515 | 1,792 | 58 | 14 | 15 | 1,280 | 896 | 59 |
| | 1.00 | 133 | 2,450 | 2,233 | 52 | 14 | 15 | 1,141 | 1,135 | 50 |
| | 1.50 | 46 | 1,065 | 446 | 70 | 13 | 12 | 2,063 | 294 | 88 |
| P260 | 0.00 | 49 | 299 | 905 | 24 | 14 | 16 | 499 | 1,495 | 25 |
| | 0.25 | 43 | 580 | 857 | 40 | 15 | 16 | 745 | 1,527 | 33 |
| | 0.50 | 52 | 369 | 595 | 38 | 14 | 16 | 874 | 1,405 | 38 |
| | 0.75 | 81 | 2,320 | 817 | 74 | 15 | 15 | 1,507 | 768 | 66 |
| | 1.00 | 111 | 2,480 | 891 | 71 | 14 | 14 | 1,274 | 1,006 | 56 |
| | 1.50 | 136 | 1,869 | 849 | 69 | 13 | 15 | 1,429 | 851 | 63 |
| Pentobarbi | ital (mg/k | g) second | dose–respor | nse determi | nation | | | | | |
| P257 | 0.0 | 99 | 908 | 2,464 | 27 | 14 | 15 | 520 | 1,763 | 23 |
| - 40. | 3.0 | 164 | 1,825 | 2,334 | 44 | 15 | 14 | 858 | 1,425 | 38 |
| | 5.0 | 192 | 2,854 | 947 | 75 | 16 | 14 | 1,649 | 626 | 72 |
| | 10.0 | 83 | 1,972 | 406 | 83 | 14 | 13 | 1,725 | 606 | 74 |
| P259 | 0.0 | 109 | 469 | 3,837 | 11 | 15 | 16 | 365 | 1,905 | 16 |
| | 3.0 | 114 | 1,298 | 1,817 | 42 | 14 | 15 | 811 | 1,471 | 36 |
| | 5.0 | 180 | 3,196 | 1,562 | 67 | 15 | 16 | 1,173 | 1,092 | 52 |
| | 10.0 | 99 | 1,900 | 773 | 71 | 13 | 10 | 1,297 | 1,015 | 56 |
| P260 | 0.0 | 101 | 271 | 1,624 | 14 | 15 | 16 | 451 | 1,825 | 20 |
| | 3.0 | 124 | 1,078 | 1,305 | 45 | 15 | 16 | 884 | 1,387 | 39 |
| | 5.0 | 105 | 2,698 | 449 | 86 | 15 | 15 | 1,867 | 409 | 82 |
| | 10.0 | 69 | 2,462 | 616 | 80 | 15 | 15 | 1,841 | 440 | 81 |